

DICOTYLEDONOUS WOOD FROM THE LOWER TERTIARY OF BRITAIN

by M. CRAWLEY

ABSTRACT. Nine species of fossil wood are described from localities in south-east England and western Scotland. These include a new genus, *Eiggoxylon* gen. nov. (Rosidae: Cunoniaceae? or Eucryphiaceae?), from the Palaeocene of Eigg, Scotland, and five new species: *Plataninium brettii* sp. nov. (Eupteleaceae?, Fagaceae?, Icacinaceae? or Platanaceae?) from the Palaeocene of Mull, Scotland; *Edenoxylon? atkinsoniae* sp. nov. (Anacardiaceae) and *Sapotoxylon atkinsoniae* sp. nov. (Sapotaceae) from the Eocene of Sheppey, Kent; *Tarrietioxylon hazzeldinewarrenii* sp. nov. (Sterculiaceae) and *T. cf. hazzeldinewarrenii* from the Palaeocene of Essex; and *Ulmium elliotii* sp. nov. (Lauraceae) from the Palaeocene of the Isle of Thanet, Kent. Also discussed are specimens from the Palaeocene assigned to *Cercidiphylloxylon spenceri* (Brett) Pearson (1987) (Cercidiphyllaceae) from Mull; *Plataninium decipiens* Brett (1972) (Icacinaceae? or Platanaceae?) from Farnborough, Berkshire; and *Ulmium? sp.* (Lauraceae) from Newbury, Berkshire. These specimens extend the geographical and lithostratigraphical range of these taxa, and provide additional information on their variability. The Scottish woods show well-defined growth rings and low vulnerability indices whilst most of the English woods have poorly defined or no growth rings and high vulnerability indices. This study complements previous research on British Palaeogene fruit, seed and leaf floras and establishes further continuity with fossil wood floras of continental Europe and North America. The fossils of Lauraceae, Sapotaceae and Sterculiaceae are first wood records for these families from the British Isles. The name *Ulmium wheelerae* nom. nov. is established for *Ulmium parenchymatosum* Wheeler, Scott and Barghoorn (1977) non Schönfeld (1956).

PRIOR to the present study in marked contrast to the large number from the Tertiary of continental Europe and North America, few dicotyledonous woods have been described from the Tertiary of Britain. Such material is important botanically in its own right as a palaeoclimatic indicator and because of the importance of the British Palaeogene fruit and seed floras (e.g. Chandler 1961–64; Reid and Chandler 1933). To date, Brett (1956–72) has described *Cercidiphylloxylon spenceri* (Cercidiphyllaceae), *Quercinium porosum*, *Q. pasanoides* (Fagaceae), *Edenoxylon aemulum* (Anacardiaceae), *Plataninium decipiens* (Platanaceae?) and *Platanus* sp. (Platanaceae) from Palaeocene and Eocene formations (Thanet Beds, Woolwich Beds, London Clay) of south-east England. Wilkinson (1984, 1988) has described pyritized twigs of *Plataninium* sp. and *Sapindoxylon* sp. (Sapindaceae) from the Eocene (London Clay) of Sheppey, Kent. Also Seward and Holttum (1924) mentioned a possible betulaceous wood from the Palaeocene of Mull. The nine species of wood described below include a new genus, *Eiggoxylon* (Cunoniaceae? or Eucryphiaceae?) and five other new species. Three other woods are included because of the new information they provide on geographical and lithostratigraphical occurrences and on variation within a taxon. The British fossil woods in this study occur over a much wider geographical area than those previously described, including specimens from the Palaeocene of Scotland (the Isles of Eigg and Mull, Inner Hebrides) as well as south-east England. The specimens are all in the collections of the British Museum (Natural History), London, some since the turn of the century whilst others have been collected in recent years.

MATERIAL AND METHODS

All the specimens are of mature wood and are either silicified or calcified. Thin sections in transverse, tangential and radial orientations were studied using a Leitz Ortholux compound microscope. Number of vessels per unit area (mm²) was calculated by counting all individual vessels including those in groups or clusters. Percentages

of solitary vessels per unit area (mm^2) were also calculated from total individual vessel counts. Quantitative ranges and means are based on at least twenty measurements where possible. Ray type is that proposed by Kribs (1950–1959). 'Anatomy of the Dicotyledons' (Metcalf and Chalk 1950) was used as a basis for comparison with extant families unless otherwise specified. Searches for various combinations of features found in the fossils, using the computerized Oxford/PRL/NCSSU database (Wheeler *et al.* 1986), were also conducted in the extant flora.

SYSTEMATIC PALAEONTOLOGY

Class MAGNOLIOPSIDA Cronquist, Takhtajan and Zimmermann (1966)

Family ANACARDIACEAE Lindley (1830)

Genus EDENOXYLON Kruse (1954)

Type species. *Edenoxylon parviareolatum* Kruse (1954) from the Eocene Green River Formation of Eden Valley, Wyoming, USA.

Edenoxylon? atkinsoniae sp. nov.

Plate 70, figs. 2–6, 10; Table 1

Derivation of name. After the collector, Mrs P. Atkinson.

Holotype. V.62710, slides V.62710\$1,2 (Pl. 70, figs. 3–5).

Paratypes. BM(NH) V.62707, slides V.62707\$1,2; V.62708, slides V.62708\$1,2; V.62709, slides V.62709\$1,2 (Pl. 70, figs. 2, 6, 10).

Locality and horizon. Collected loose from the beach, Isle of Sheppey, Kent; Lower to Middle Eocene, London Clay.

Diagnosis. [Secondary xylem and bark]. Vessels diffuse porous, 20–28/ mm^2 , solitary and in radial multiples of 2–15, tangential diameter means 63–105 μm , element length means of 410–470 μm . Perforation plates simple. Intervascular pitting alternate and bordered, pits 6 μm in diameter; vessel to ray/parenchyma pitting round to elongate and possibly simple, up to 12 μm diameter. Parenchyma often absent, if present as incomplete vasicentric sheaths. Rays mainly biseriate with uniseriate rays moderately common; distribution en échelon. Multiseriate portions of rays often no wider than uniseriate portions. Ray width means 18–21 μm (1–2 cells), uniseriate ray height means 100–160 μm (4–5 cells), multiseriate ray height means 245–330 μm (7–11 cells), heterogeneous type II, multiseriate rays usually with marginal rows of 1–4, square to upright cells, uniseriate rays composed of upright and square cells. Fibres libriform and septate with thin walls. Bark consisting of concentric bands of thin- and thick-walled cells containing axial canals.

Description. Four calcified specimens, the largest 24 cm diameter by 4 cm thick before cutting. Much of the wood structure has been destroyed by *Teredo* burrows. Only very vague evidence of incremental growth.

Vessel elements (Table 1): solitary (50%) and in radial multiples of 2–15 (Pl. 70, fig. 3), the longer multiples present locally, consisting of irregular sized vessels (Pl. 70, fig. 4); vessel to ray/parenchyma pitting usually poorly preserved, alternate, bordered, round to slit-like (Pl. 70, fig. 10); thin-walled tyloses present in many vessels.

Parenchyma: usually absent, rarely present as incomplete vasicentric sheaths (V.62710).

Rays (Table 1): 4–6 rays per tangential mm; predominantly biseriate (70–80%) with uniseriate rays moderately common; multiseriate portions of rays composed of procumbent cells, uniseriate ray margins of 1–7 (usually 1–4) square and upright cells (Pl. 70, figs. 5 and 6); a few crystals present in ordinary marginal cells.

Imperforate tracheary elements: libriform fibres in radial file; septate; 15–18 μm diameter (length not determinable due to poor preservation); thin-walled; pitting not observed.

TABLE 1. Variability in quantitative features of *Edenoxylon atkinsoniae* sp. nov. TD = tangential diameter; EL = element length; RW = ray width; MH = multiseriatic height; UH = uniseriate height.

	V.62707	V.62708	V.62709	V.62710
Vessels				
TD mean (μm)	63	98	84	105
TD range	42–70	56–140	28–140	53–148
EL mean (μm)	410	415	—	470
EL range	280–560	256–585	—	350–600
Rays				
RW mean (μm)	18	19	19	20
RW range	16–21	17–22	17–23	17–23
RW range (cells)	1–2	1–2	1–2	1–3
MH mean (μm)	245	300	330	240
MH range	140–350	170–400	200–420	140–420
MH mean (cells)	11	10	11	7
MH range	7–13	7–17	10–17	6–16
UH mean (μm)	160	170	—	100
UH range	130–270	100–200	200–280	60–210
UH mean (cells)	5	5	—	4
UH range	4–9	3–8	4–5	2–7

Bark: (Pl. 70, fig. 2) alternate zones of thick-walled cells, probably sclerenchyma and thin-walled cells with many axial canals containing a black to reddish substance, possibly the remains of gum or resin.

Comparison. Woods with axial parenchyma either absent or present only as rare, incomplete, vasicentric sheaths together with septate fibres and vertical canals in the bark occur only in Anacardiaceae and Burseraceae. Some extant genera in both families show a broad similarity to the fossils. In Burseraceae the ray margins are never more than four cells high and are heterogeneous III, differing from the fossils. However Anacardiaceae agree with the fossils in these features and although a close match with a living genus could not be made, the preserved features of the Sheppey woods indicate affinity with this family.

Of the fossil woods assigned to Anacardiaceae, only species in the genera *Anacardioxylon* Felix (1882), *Holigarnoxylon* Prakash and Awasthi (1970), *Mangiferoxylon* Awasthi (1966), *Rhoidium* Unger (1850) and *Rhus crystallifera* Wheeler, Scott and Barghoorn (1978) lack radial canals in the rays. However none of these is closely comparable with the Sheppey fossils. The closest comparison can be made with three species that have canals in the rays. These are *Edenoxylon aemulum* Brett (1966) from the Upper Palaeocene Woolwich Beds of Herne Bay, Kent (the only other anacardiaceous fossil wood recorded from the British Isles); *E. parviareolatum* Kruse (1954) from the Eocene of Eden Valley, Wyoming, USA, and *Tapirira clarnoensis* Manchester (1977) from the Upper Eocene Clarno Nut Beds of Eastern Oregon, USA. *T. clarnoensis* has a lower density of vessels (8–13 per mm^2) and commoner vasicentric parenchyma, *E. parviareolatum* has exclusively uniseriate rays and very small vessels, and *E. aemulum* has a greater density of vessels, rays that are mainly heterogeneous III, and large, fusiform rays containing radial canals.

Remarks. *Edenoxylon* was erected for fossil woods having affinities with Anacardiaceae but not comparable with any one Recent genus. A feature of the original description was the presence of radial canals. *Edenoxylon? atkinsoniae*, as mentioned earlier, lacks these canals. However in the Recent genera radial canals may not be present in all species of a genus, e.g. *Pseudospondias*, *Rhus*. *Edenoxylon? atkinsoniae* is very similar in other respects to *E. aemulum* and to a lesser extent *E. parviareolatum*. *Edenoxylon? atkinsoniae* is not closely comparable with any Recent genus but

the possession of sparse, paratracheal parenchyma, vessels commonly in radial groups, and septate fibres shows it to be most similar to the tribes Spondiæ and Rhoideæ of Anacardiaceæ. Both these tribes have previously been recognized in the London Clay flora from wood (Brett 1966), fruits (Reid and Chandler 1933) and pollen (Sein 1961).

Present-day Anacardiaceæ is an arborescent, tropical family. *Edenoxylon? atkinsoniae* with its diffuse porous vessels and, at most, extremely vague evidence of seasonal growth is typically tropical. As such it is climatically consistent with other elements of this flora, for which the nearest Recent analogue is paratropical rain forest (Collinson 1983).

Family CERCIDIPHYLLACEAE Engler (1909)

Genus CERCIDIPHYLLOXYLON Prakash, Březinová and Bůžek (1971)

Type species. Cercidiphylloxylon kadanense, from the Oligocene Volcanogenic Complexes of Kadan (Zadni vrch Hill), Doupovské Hory Mountains, North Bohemia, Czechoslovakia.

Cercidiphylloxylon spenceri (Brett) Pearson (1987)

Plate 69, figs. 1–6; Table 2

- 1956 *Cercidiphyllum spenceri* Brett; pp. 658–661, pl. 21, text-fig. 1.
- 1977 *Cedroxylon* sp.; Creber, pp. 367–368, 370, fig. 4g.
- 1982 *Cercidiphyllum alalongum* Scott and Wheeler; pp. 137–138, figs. 11–15.
- 1987 *Cercidiphylloxylon spenceri* (Brett) Pearson; p. 59.

Material. BM(NH) V.58746, slides V.58746\$1,2; BM(NH) V.60312, slides V.60312\$1–5 (Pl. 69, figs. 1–6).

Locality and horizon. Loose on the beach at Ardalanish, Mull, Inner Hebrides; Palaeocene, Interbasaltic Beds, Plateau Volcanics Series.

Description. Two calcified specimens, the largest (V.58746) measuring 13 cm × 14 cm × 12 cm before cutting. All measurements from the Holotype. Conspicuous growth rings, 1.5–2 mm wide.

Vessel elements: diffuse porous, but with a gradual decrease in size across the growth ring (Pl. 69, fig. 1); mostly solitary with some radial alignment, multiples with both radial and tangential alignment (Pl. 69, fig. 2), vessels angular in cross-section, predominantly solitary, up to 180/mm², tangential diameter range 28–70 µm, mean tangential diameter 55 µm, element length range 630–1400 µm, mean element length 1000 µm; perforation plates scalariform with 30–55 fine bars, some reticulate perforation plates (Pl. 69, fig. 5); intervacular and vessel to ray pitting opposite, round, elongate to scalariform (near perforation plates), simple to half-bordered, 6–30 µm in diameter, occasional unilaterally compound pits present; some vessels contain a brown substance that was probably gum.

Parenchyma: none could be identified.

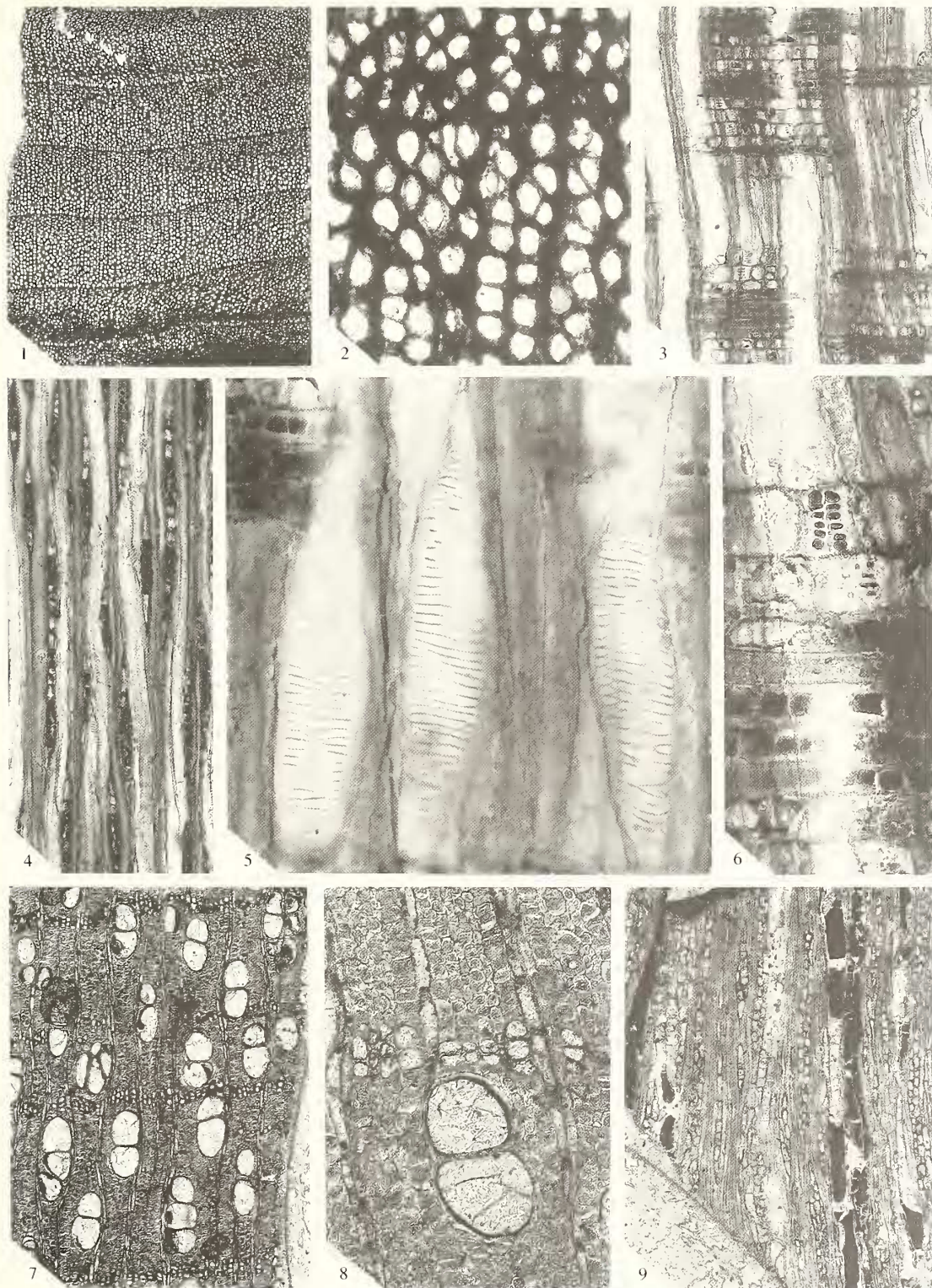
Rays: 7–10 per tangential mm; predominantly 2 cells wide, very rarely uniseriate, distinctive in form, many having more than one biseriate portion and rarely up to five such portions; often these portions are no wider

EXPLANATION OF PLATE 69

TS = transverse section; RLS = radial longitudinal section; TLS = tangential longitudinal section throughout plates.

Figs. 1–6. *Cercidiphylloxylon spenceri* (Brett) Pearson (1987) from Mull, Inner Hebrides, Scotland, Palaeocene, Interbasaltic Beds. Thin sections. 1, V.60312\$2, TS, × 6.5. 2, V.60312\$2, TS, detail across a growth ring boundary, × 68. 3, V.60312\$3, RLS, × 68. 4, V.60312\$1, TLS, × 71. 5, V.60312\$3, RLS, scalariform and reticulate perforation plates, × 272. 6, V.60312\$3, RLS, vessel to ray pitting, × 289.

Figs. 7–9. *Sapotoxylon atkinsoniae* sp. nov. from the Isle of Sheppey, Kent, England, London Clay, Eocene. Thin sections. 7, BM(NH) V.62706\$2, holotype, TS, × 42. 8, BM(NH) V.62706\$2, holotype, TS, detail of parenchyma band showing three cell width, × 170. 9, BM(NH) V.62705\$2, paratype, TLS, × 68.



CRAWLEY, *Cercidiphyllaxylon*, *Sapotoxylon*

than the uniseriate portions of the ray (Pl. 69, fig. 4); width range 22–27 μm (1–2 cells), mean ray width 25 μm (1–2 cells), multiseriate ray height range 140–1100 μm (5–36 cells), multiseriate ray height mean 450 μm (18 cells); uniseriate ray height range 100–200 μm (2–8 cells); heterogeneous type I–II, marginal rows of 1–9, usually 1–4, square and upright cells, uniseriate rays composed of square and upright cells; marginal cells often contain a single rhomboidal crystal; multiseriate portions of rays containing a brown substance, probably the remains of gum.

Imperforate tracheary elements: fibre-tracheids; tangential diameter range 7–14 μm , length range 840–1400 μm , mean 1100 μm , medium to thick-walled; distinctly bordered pits present on radial walls.

Comparison. The arrangement of the vessels and particularly the structure of the rays indicate affinity with Recent *Cercidiphyllaceae* (C) or *Hamamelidaceae* (H), especially the genera *Cercidiphyllum* (C), *Corylopsis* (H) and *Liquidambar* (H). Previous comparative studies on the wood anatomy of *Cercidiphyllum japonicum* Siebold and Zuccarini (1846), *Corylopsis* spp. (Swamy and Bailey 1949; Brett 1956; Scott and Wheeler 1982) and *Liquidambar* spp. (Prakash *et al.* 1971) show that secondary wood of *Cercidiphyllum* can be separated from that of *Corylopsis*/*Liquidambar* by differences in ray structure. The possession of commonly three biseriate portions per ray with the uniseriate portions of the ray often no wider than the multiseriate portions show the Mull woods to be most similar to *Cercidiphyllum*.

In Table 2, three specimens of *Cercidiphyllaxylon spenceri* are compared with *C. kadanense*. They are similar in many features but are distinguishable by the presence of triseriate rays and larger diameter vessels in *C. kadanense*. However also in *C. kadanense* some important diagnostic features are missing due to poor preservation, i.e. intervascular, vessel to ray or axial parenchyma, and fibre pitting. For the present I regard these species as distinct not only because of the features noted above but also because of the lack of knowledge regarding variation in fossil and Recent cercidiphyllaceous woods.

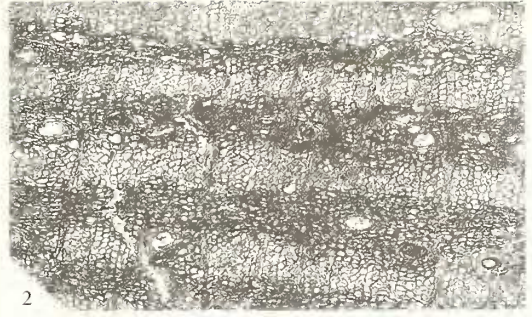
Remarks. Few cercidiphyllaceous woods have been described. Four of these are compared in Table 2. As can be seen, only minor qualitative and quantitative differences separate BMNH V.23438–9, V.60312 and USNM 326701 (described as *Cercidiphyllum alalongum* Scott and Wheeler, 1982). In Recent wood variation of this type can be interspecific or intraspecific. In the latter this is due to: (a) the relative age of different parts of the tree, i.e. twig wood and trunk heart wood; (b) the position of equally mature wood on the tree, i.e. branch, trunk or root; (c) the effect of ecological controls on growth, i.e. altitude, soil. A necessarily cautious approach is needed regarding the interpretation of such variation in fossil taxa based solely on wood especially as little is known about such variation in Recent *Cercidiphyllum*. As mentioned previously the differences between the samples of *Cercidiphyllaxylon spenceri* are not substantive. They are interpreted as probably intraspecific variation between the twig/small branch and main axial wood represented by the specimens.

EXPLANATION OF PLATE 70

Figs. 1–9. *Sapotoxylon atkinsoniae* sp. nov. from the Isle of Sheppey, Kent, England, London Clay, Eocene. Paratype. Thin sections. 1, BM(NH) V.62704\$1, RLS, $\times 68$. 9, BM(NH) V.62704\$1, RLS, chambered, crystalliferous cells in parenchyma strand, $\times 289$.

Figs. 2–6, 10. *Edenoxylon? atkinsoniae* sp. nov. from the Isle of Sheppey, Kent, England, London Clay, Eocene. Thin sections. 2, BM(NH) V.62709\$2, paratype, TS, bark, $\times 42$. 3, BM(NH) V.62710\$1, holotype, TS, $\times 17$. 4, BM(NH) V.62710\$1, holotype, TS, detail of vessel chains, $\times 68$. 5, BM(NH) V.62710\$2, holotype, TLS, $\times 170$. 6, BM(NH) V.62709\$1, paratype, RLS, $\times 68$. 10, BM(NH) V.62709\$1, paratype, RLS, vessel to ray pitting, $\times 289$.

Figs. 7, 8. *Ulmium?* sp. from Shaw, Berkshire, England, Reading Beds, Palaeocene. Thin sections. 7, BM(NH) V.24\$1, TS, $\times 17$. 8, BM(NH) V.24\$2, TLS, showing oil or mucilage idioblasts? at ray margins, $\times 42$.



CRAWLEY, *Sapotoxylon*, *Edenoxylon*?, *Ulmimum*?

TABLE 2. Comparison of quantitative and qualitative features for specimens of *Cercidiphylloxylon spenceri* (CSp) and *C. kadanense* (CKa).

	CSp Scott and Wheeler 1982 USNM 326701	CSp Brett 1956 V.23438-39	CSp this study V.60312	CKa Prakash <i>et al.</i> 1971 ZV-12
Primary wood				
Central pith cells	More or less square, 20–50 μm	More or less square, 30 μm	—	—
Marginal pith cells	Axially elongate, 15 $\mu\text{m} \times 40 \mu\text{m}$	Axially elongate, 10–15 $\mu\text{m} \times 24\text{--}60 \mu\text{m}$	—	—
Secondary wood				
Growth rings	Present	Present	Present	Present
Vessel density (/mm ²)	Up to 150	Up to 160	Up to 180	Up to 110
Vessel diameter (μm)	22–25	—	28–70	32–88
Perforation plates	Mean 35	Mean 40	Mean 55	No details
	Scalariform	Scalariform	Scalariform	Scalariform
	20–50 bars, occasionally reticulate	25–30 bars occasionally reticulate	30–55 bars, occasionally reticulate	30+ bars
Pitting	Opposite to scalariform	Opposite to scalariform	Opposite to scalariform	Not preserved
Axial parenchyma	Not observed	Present, diffuse or scanty paratracheal?	Not observed	Present? diffuse or scanty paratracheal?
Ray width (cells)	1–2	early wood 1–2	1–2	1–3
Ray margins (cells)	1–9	1–7	1–9	No details
Crystalliferous cells	Present, rays	Present, ray margins and parenchyma	Present, ray margins	No details
Fibre-tracheids	Present	Present	Present	Libriform fibres?

Cercidiphyllum-like leaves and fructifications are common and widespread in Upper Cretaceous and Palaeogene strata, and belong to a diverse group of several taxa (Crane 1984; Crane and Stockey 1985).

Present-day *Cercidiphyllum* is a relic genus restricted to China and Japan, as part of a temperate flora.

The two specimens of *C. spenceri*, although found loose on the beach, are almost certainly from the Palaeocene age Interbasaltic Beds present on Mull. They are the first examples of cercidiphyllaceous wood recorded from this region. *Cercidiphyllum*-like leaves are common in the Interbasaltic flora of Ardtun Head, Mull.

Family CUNONIACEAE? R. Brown in Flinders 1814 or EUCRYPHIACEAE? Endlicher (1841)

Genus EIGGOXYLON gen. nov.

Type species. Eiggoxylon reidii sp. nov. from the Palaeocene Plateau Volcanic Series of Eigg, Inner Hebrides.

Diagnosis. [Secondary xylem]. Distinct growth rings present. Vessels semi ring porous. Both simple and scalariform perforation plates present. Vessel to ray/parenchyma pitting alternate to opposite, round and elongate. Rays of two sizes, homogeneous to heterogeneous type III. Fibre-tracheids present.

Derivation of name. After the Scur of Eigg, where the specimen was found.

Eiggoxylon reidii sp. nov.

Plate 71, figs. 5–10

Derivation of name. After the collector, the late Mr Clement R. Reid.

Holotype. BM(NH) V.59122, slides V.59122\$1–12 (Pl. 71, figs. 5–10).

Locality and horizon. (Probably collected loose.) Scur of Eigg, Inner Hebrides; probably from the Palaeocene Interbasaltic Beds, Plateau Volcanics Series.

Diagnosis. [Secondary Xylem]. Growth rings 2.5–4.5 mm wide. Vessels 30/mm² in early part of ring to 40/mm² in late part of ring; solitary; tangential diameter range 14–154 µm, length mean 410 µm; perforation plates are simple in larger vessels, scalariform in smaller, with 12–20 bars. Vessel to ray pitting of two types, either round or elongate, usually with distinct borders. Rays 6–7 per tangential mm, of two distinct sizes, uniseriate or three to four seriate, uniseriate ray height mean 110 µm (7 cells), multiseriate ray height mean 250 µm (16 cells), homogeneous to weakly heterogeneous III. Fibre-tracheids with distinctly bordered pits.

Description. A single silicified specimen, 11 cm × 2.5 cm × 5 cm.

Vessel elements: density 22–32/mm² in early wood, 32–42/mm² in late wood (Pl. 71, figs. 5 and 6); element length range 200–560 µm; intervacular pitting not observed due to solitary vessels; elongate vessel to ray pits usually horizontally aligned, but can be almost vertical; some elongate pits unilaterally compound; round pitting diameter 3–5 µm, elongate pitting up to 22 µm in length (Pl. 71, fig. 9); abundant tyloses in the larger vessels of the early wood.

Parenchyma: probably apotracheal, diffuse (not observed in transverse section, solitary strands seen in tangential section).

Rays: of two distinct sizes, each comprising approximately 50% of total (Pl. 71, fig. 8); uniseriate ray height range 33–330 µm (2–17 cells), multiseriate ray height range 84–420 µm (5–29 cells), mean 250 µm (16 cells); uniseriate ray width range 5–12 µm, mean 7 µm; multiseriate rays width range 12–50 µm (2–4 cells), mean

35 μm (3–4 cells); mainly homogeneous and in some areas weakly heterogeneous type III, marginal rows usually of 1–2 cells but sometimes up to 4 cells (Pl. 71, figs. 7 and 8).

Imperforate tracheary elements: fibre-tracheids; tangential diameter range 15–24 μm (length not determinable due to poor preservation); thin-walled; distinctly bordered pits present on the radial walls; possible presence of vascular tracheids in a few areas adjacent to vessels; irregularly arranged cells with what appears to be more than one row of bordered pits.

Comparison. The main features of the Eigg wood are its semi ring porous structure, solitary vessels, fibres with distinctly bordered pits, and the presence of both simple and scalariform perforation plates. These features occur in sixteen extant families of which Cunoniaceae and Eucryphiaceae are the most similar to the fossil. The presence of scalariform perforation plates in the smaller vessels is characteristic of some genera in Cunoniaceae whilst round and horizontally elongate vessel to ray pitting is more typical of Eucryphiaceae. However, a clear distinction cannot usually be made between the families in terms of wood anatomy (Record and Hess 1943), and Bausch (1938) has implied close relationship of Cunoniaceae and Eucryphiaceae on this basis. The fossil differs from both families in ray structure, having rays that are predominantly homogeneous as opposed to characteristically heterogeneous III (though extant *Ceratopetalum* (C) is recorded as having homogeneous rays). It should also be remarked that the gross anatomy of the fossil is very similar to some species of *Malus* and *Sorbus* (Rosaceae), although the perforation plates, intervacular pitting and vessel to ray pitting differ markedly. The fossil is therefore regarded as showing general affinity with the Rosidae as a whole and tentatively with Cunoniaceae and Eucryphiaceae.

I know of no other fossil wood that compares closely with the Eigg fossil. The only species with affinity to Cunoniaceae, *Cunonioxylon weinmannioides* Hofmann (1952) from the Oligocene of Prambachkirchen, Austria, differs from the Eigg wood in having diffuse porous vessels with paratracheal and marginal parenchyma.

Remarks. Other possible rosid remains in the Interbasaltic Flora are the leaf *Vitiphyllum* from the Ardtun Leaf Beds of Mull. Only one other wood is known from the Palaeocene of Eigg, the coniferalean *Pityoxylon eigense* (Witham) Kraus (1870).

Ring porous woods are not common prior to the Oligocene (Wheeler *et al.* 1987). The probable Palaeocene age of *Eiggoxylon* makes it one of the earliest known stratigraphical occurrences.

Family LAURACEAE A. L. Jussieu (1789)

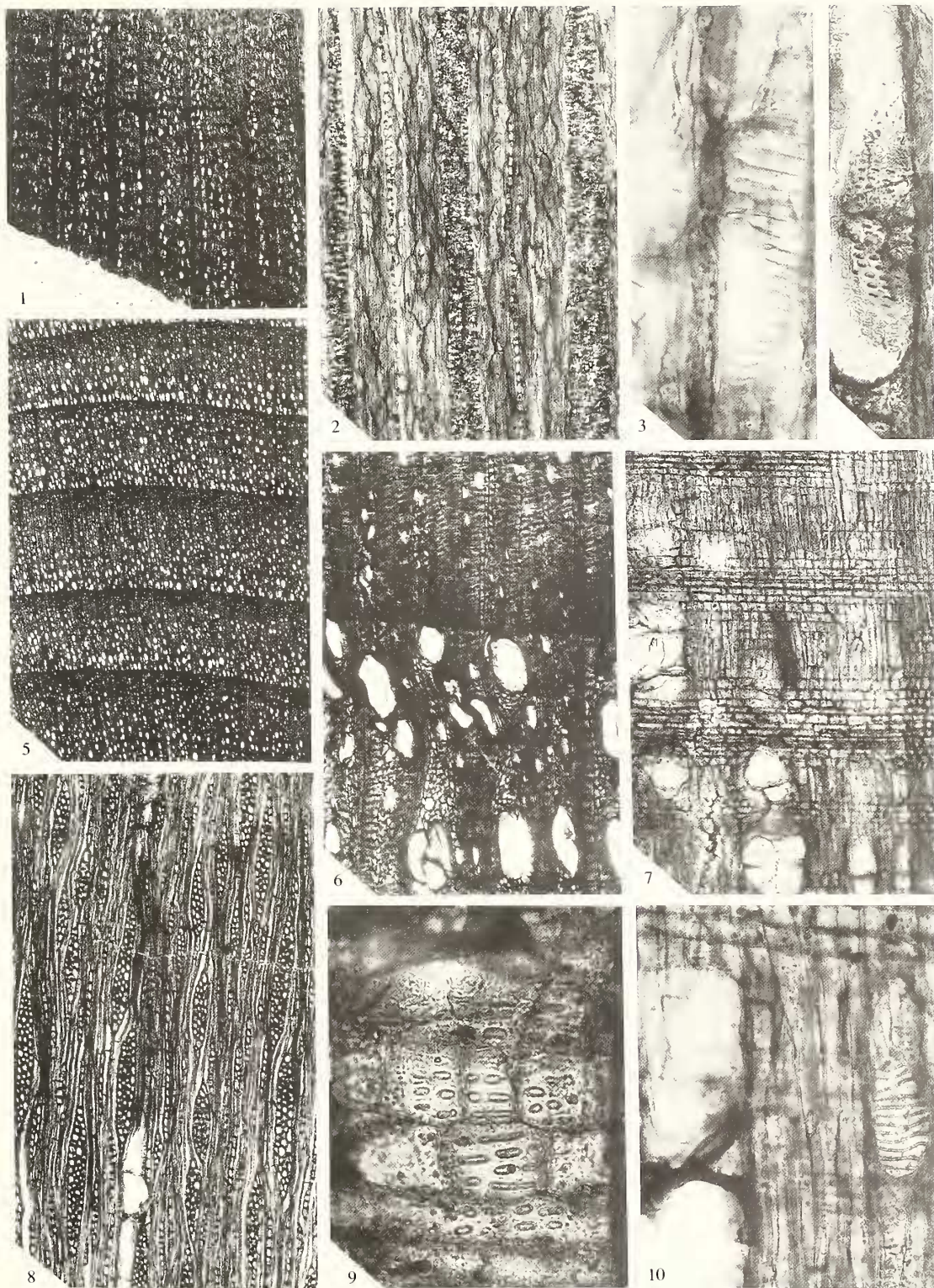
Genus ULMINIUM Unger (1842)

Type species. *Ulmium diluviale* Unger (1842) from the Tertiary of Bohemia, Czechoslovakia.

EXPLANATION OF PLATE 71

Figs. 1–4. *Plataninium brettii* sp. nov. from Mull, Inner Hebrides, Scotland, Palaeocene, Interbasaltic Beds. Holotype. Thin sections. 1, BM(NH) V.25264\$1, TS, showing a single growth ring boundary, $\times 17$. 2, BM(NH) V.25264\$3, TLS, long uniseriate rays alternating with multiseriate rays, $\times 68$. 3, BM(NH) V.25264\$2, RLS, scalariform perforation plate, $\times 272$. 4, BM(NH) V.25264\$2, RLS, opposite and alternate vessel to ray pitting, $\times 289$.

Figs. 5–10. *Eiggoxylon reidii* sp. nov. from Eigg, Inner Hebrides, Scotland, Palaeocene, Interbasaltic Beds. Holotype. Thin sections. 5, BM(NH) V.59122\$8, TS, $\times 6.5$. 6, BM(NH) V.59122\$8, TS, detail across a growth ring boundary, $\times 68$. 7, BM(NH) V.59122\$10, RLS, $\times 71$. 8, BM(NH) V.59122\$9, TLS, $\times 71$. 9, BM(NH) V.59122\$10, RLS, vessel to ray pitting, $\times 464$. 10, BM(NH) V.59122\$10, RLS, on the right is a small vessel with a scalariform perforation plate, on the left is a large vessel with a simple perforation plate.



CRAWLEY, *Plataninium*, *Eigoxylon*

Ulmium elliottii sp. nov.

Plate 72, figs. 1–6; Table 3

Derivation of name. After Dr Graham F. Elliott, head of the Fossil Plant Section at the British Museum (Natural History), 1968–81.

Holotype. V.8364(1–3) (Pl. 72, figs. 1–3, 5). Slide.

Paratypes. BM(NH) V.8358(1–3), V.8359(1–3), V.8363(1–3) (Pl. 72, figs. 4 and 6). All are slides.

Other material. BM(NH) V.8369–8375(2), V.8376–V.8381, V.63117. All are slides.

Locality and horizon. 'Isle of Thanet' (Pegwell Bay or Reculvers?), Kent; probably from the Palaeocene Thanet Sands, Woolwich Beds or Oldhaven Beds. These specimens were transferred to the Palaeontology Department from the Botany Department in 1898 with no accompanying data other than 'Isle of Thanet'.

Diagnosis. [Secondary wood]. Growth rings distinct, 3–4 mm wide. Vessels diffuse porous, 6–12/mm², mainly solitary, tangential diameter means 135–147 μ m, element length means 350–420 μ m; perforation plates simple; intervacular pitting alternate, bordered, diameter 7–8 μ m; vessel to ray/parenchyma pitting simple, alternate, round to elongate, diameter up to 26 μ m. Parenchyma paratracheal, vasicentric. Rays 4 per tangential mm, commonly multiseriate, up to 7 cells wide; uniseriate rays few and low, ray width means 50–60 μ m (4–5 cells), multiseriate ray height means 560–600 μ m (25–28 cells), uniseriate ray height means 170–200 μ m (3–4 cells); heterogeneous type III, uniseriate rays composed of square to upright cells. Fibres libriform, thin walled. Oil or mucilage idioblasts present amongst the fibres, up to 32/mm², occurring singly and in small groups of two to four, diameter up to 42 μ m, length up to 420 μ m.

Description. Vessel elements (Table 3): diffuse porous with only a gradual change in size across growth ring (Pl. 72, fig. 1); 6–12 (usually 9)/mm²; mainly solitary with some radial groups of 2–3 cells (Pl. 72, fig. 2); vessel to ray/parenchyma pitting alternate to almost scalariform (Pl. 72, fig. 6); thin-walled tyloses present.

Parenchyma: paratracheal, as moderately complete vasicentric sheaths, 1–3 cells across (Pl. 72, fig. 2).

Rays (Table 3): 3–5 (mostly 4) per tangential mm; predominantly multiseriate and up to 7 cells wide; uniseriate rays scarce, usually not more than 4 cells high, rarely up to 7 cells high; multiseriate portions of rays composed of procumbent cells with marginal rows of 1–2 square to upright cells (Pl. 72, figs. 4 and 5).

Imperforate tracheary elements: libriform fibres in radial rows; 15–20 μ m tangential diameter, length range 640–820 μ m, mean 623 μ m (V.8358), 500–800 μ m, 600 μ m (V.8363), 550–678 μ m, 635 μ m (V.8364); thin-walled; pitting not observed. (What appear initially to be septae are fungal hyphae which pass horizontally, or nearly so, through the fibres.)

EXPLANATION OF PLATE 72

Figs. 1–6. *Ulmium elliottii* sp. nov. from Thanet, Kent, England, Palaeocene, Thanet Sands, Woolwich Beds or Oldhaven Beds? Thin sections. 1, BM(NH) V.8364(1), holotype, TS, $\times 6.5$. 2, BM(NH) V.8364(1), holotype, TS, showing oil or mucilage idioblasts amongst the fibres, $\times 42$. 3, BM(NH) V.8364(1), holotype, TLS, oil or mucilage idioblast showing spindle shape, $\times 71$. 4, BM(NH) V.8363(1), paratype, RLS $\times 170$. 5, BM(NH) V.8364(1), holotype, TLS, $\times 71$. 6, BM(NH) V.8363(1), paratype, TLS, vessel to parenchyma pitting, $\times 289$. Eocene.

Figs. 7, 9–11. *Tarrietioxylon hazzeldiniwarrenii* sp. nov. from Nazeing, Essex, England, Palaeocene, Reading Beds. Holotype. Thin sections. 7, BM(NH) V.28223\$4, TLS, sheath cells can be seen in the multiseriate rays, $\times 29$. 9, BM(NH) V.28223\$1, TS, note uniseriate lines of parenchyma extending from ray to ray in the top half of figure, $\times 17$. 10, BM(NH) V.28223\$2, RLS, showing part of a single ray, $\times 68$. 11, BM(NH) V.28223\$2, RLS, vessel to parenchyma pitting with coalescent apertures, $\times 464$.

Fig. 8. *Tarrietioxylon* cf. *hazzeldiniwarrenii*, from Nazeing, Essex, England, Palaeocene, Reading Beds. Thin section. BM(NH) V.28222\$2, TLS, $\times 29$.



CRAWLEY, *Ulmimum*, *Tarrietioxylon*

TABLE 3. Variability in quantitative features of *Ulmium elliotii* sp. nov. TD = tangential diameter; EL = element length; RW = ray width; MH = multiseriata height; UH = uniseriate height.

	V.8358	V.8359	V.8363	V.8364
Vessels				
TD mean (μm)	140	138	135	147
TD range	56–196	70–189	50–168	56–198
EL mean (μm)	350	336	420	400
EL range	168–560	150–420	156–560	175–578
Rays				
RW mean (μm)	56	50	56	54
RW range	28–98	20–70	28–84	25–90
RW range (cells)	4	5	4	4
RW range	1–7	1–6	1–6	1–7
MH mean (μm)	600	580	560	578
MH range	196–1116	160–1640	150–1400	156–1260
MH mean (cells)	28	30	27	25
MH range	7–55	9–73	5–66	6–63
UH mean (μm)	200	180	175	170
UH range	70–260	55–220	100–240	60–270
UH mean (cells)	4	3	4	4
UH range	2–6	2–6	3–8	1–8

Oil or mucilage idioblasts: 2–32/mm² (Pl. 72, fig. 2); diameter 21–42 μm , length up to 420 μm ; elongate spindle-shaped (Pl. 72, fig. 3); extremely thin-walled; no obvious contents.

Comparison. The presence of oil or mucilage idioblasts is an important diagnostic feature of woods (see list in Metcalfe and Chalk 1950, p. 1354). When compared with the Thanet woods only Lauraceae exhibit identical major features. Richter (1987) commented that oil or mucilage idioblasts isolated in the fibrous tissue is a characteristic of the family and that these idioblasts are sometimes of similar size and shape to the surrounding libriform fibres (as found in *Ulmium elliotii*). In Recent genera they most commonly occur in *Beilschmiedia*, *Cryptocarya*, *Endiandra* and in some species of *Actinodaphne*, *Cinnamomum*, *Endlicheria*, *Nectandra*, *Neolitsea*, *Ocotea* and *Ravensara*. This type of idioblast is most commonly a mucilage rather than an oil cell, a distinction based on cell content. Considering all the characters *U. elliotii* seems to be most similar to the Recent genus *Beilschmiedia*, which has some species with rays up to eight cells in width and others with a comparable distribution of idioblasts but differs in usually having aliform to confluent parenchyma.

Many fossil lauraceous woods have been described (Süss 1958; Süss and Mädel 1958). Only three share with *U. elliotii* the occurrence of idioblasts exclusively or predominantly in the ground tissue: *U. deomaliensis* Lakhanpal, Prakash and Awasthi (1981), from the Mio-Pliocene Namsang Beds of Deomali, Arunachal Pradesh, India; *U. eocenicum* Wheeler, Scott and Barghoorn (1977); and *U. wheelerae* (see below), both from the late early to early middle Eocene Lamar River Formation of Specimen Ridge, Yellowstone National Park, Wyoming, USA. *U. deomaliensis* has larger, barrel-shaped idioblasts (40–100 μm in diameter), rays only three cells broad, and a smaller vessel diameter (60–120 μm), *U. wheelerae* possesses abundant vasicentric, aliform and aliform-confluent parenchyma, and *U. eocenicum* has marginal parenchyma delimiting growth-rings and idioblasts of a lower density (1–2/mm²).

Remarks. As indicated by Page (1967–8), *Ulmium* Unger (1842) takes precedence over *Laurinoxylon* Felix (1883) for fossil woods of lauraceous affinity. This creates the name *Ulmium*

(*Laurinoxylon*) *parenchymatosum* Schönfeld (1956) which predates *Ulmium* *parenchymatosum* Wheeler, Scott and Barghoorn (1977), now an invalid homonym. Therefore the new species name *U. wheelerae* nom. nov. is erected here.

Ulmium wheelerae nom. nov.

1977 *Ulmium parenchymatosum* Wheeler, Scott and Barghoorn (non Schönfeld, 1956); holotype, p. 289, figs. 12–14.

Derivation of name. After Professor Elisabeth A. Wheeler in recognition of her work on fossil dicotyledonous wood floras of the USA.

Ulmium? sp.

Plate 70, figs. 7 and 8

Material. BM(NH). V.24, slides V.24\$1–6.

Locality and horizon. *In situ*, railway cutting, Shaw, near Newbury, Berkshire; Upper Palaeocene, Reading Beds.

Collection details. Collected by Professor T. R. Jones, 1881.

Description. Single silicified piece of secondary xylem, measuring 9 cm × 4 cm × 4 cm before sectioning. No evidence of incremental growth.

Vessel elements: diffuse porous; 7–11/mm²; solitary (60%) and in radial multiples of 2–5 cells (Pl. 70, fig. 7); tangential diameter range 56–212 µm, mean 168 µm; length range 140–420 µm, mean 335 µm; intervascular pitting alternate, bordered, 11–14 µm in diameter, vessel to ray/parenchyma pitting not preserved; thin-walled tyloses present.

Parenchyma: paratracheal, vasicentric.

Rays: 4–6 per tangential mm; all the rays are multiseriate; width range 50–120 µm (2–3 cells), mean 84 µm; height range 400–1400 µm (10–31 cells), mean 900 µm (16 cells); heterogeneous type III, with multiseriate portions composed of procumbent cells, marginal rows composed of 1–2, square to upright cells (Pl. 70, fig. 8).

Imperforate tracheary elements: libriform fibres; septate; tangential diameter range 20–30 µm (length indeterminate because of poor preservation); thin-walled; pitting not observed.

Oil or mucilage idioblasts?: possible remains of large, inflated cells in ray margins and amongst fibres, very poorly preserved (Pl. 70, fig. 8).

Remarks. Several diagnostically important features are seen poorly or lacking in this wood because of its poor preservation, especially vessel to ray pitting and parenchyma, but the paucity of *in situ* fossil dicotyledonous woods from the Reading Beds justifies inclusion here. In tangential section, some rays appear to have inflated cells and they look similar to oil or mucilage idioblasts in photographs of *U. süssi* Greguss (1969) and *Cinnamomoxylon?* sp. (Greguss 1969, pl. 18, figs. 4 and 5, pl. 20, figs. 2 and 3). The possible oil or mucilage idioblasts in combination with vasicentric? parenchyma, 2–3 seriate, heterogeneous type III rays, large intervascular pitting and simple perforation plates indicate possible lauraceous affinity. It is therefore regarded (with some reservations) as an indeterminate species of *Ulmium*.

According to Chandler (1964) at least eight genera of lauraceous fruits and seeds are known from the Lower Tertiary of Britain, ranging from the Reading and Woolwich Beds to the London Clay. Both lauraceous specimens described here are diffuse porous woods and were probably growing in tropical or subtropical conditions. Present-day Lauraceae remains a tropical or sub-tropical family.

Family PLATANACEAE? Damortier (1829) or ICACINACEAE? Miers (1851)
Genus PLATANINIUM Unger (1842) emend. Brett (1972)

Type species. *Plataninium acerinum* Unger (1842) horizon and locality unknown.

Plataninium decipiens Brett (1972)

1972 *Plataninium decipiens* Brett, p. 497, pl. 99, figs. 3–6

1977 *Plataninium decipiens*; Süss and Müller-Stoll, pp. 50, 51, 57

Material. BM(NH) V.62922, slides V.62992\$1–10.

Locality and horizon. Collected loose on surface, Farnborough, Berkshire; Upper Palaeocene, Reading Beds.

Collection details. Collected by Mr A. de S. Dacrelacey, 1984.

Description. A single silicified piece, measuring 11 cm × 8.5 cm × 7 cm before cutting. Secondary xylem with no evidence of incremental growth.

Vessel elements: diffuse porous, exclusively solitary; 12–19/mm²; tangential diameter 30–100 µm, mean 75 µm; length 520–1040 µm, mean 800 µm; perforation plates scalariform with 14–24 bars; vessel to ray/parenchyma pitting scalariform, poorly preserved.

Parenchyma: apotracheal, diffuse-in-aggregate in short, uniseriate, tangential lines extending from ray to ray.

Rays: 1–2 per tangential mm; all multiseriate; width 50–560 µm (4–30 cells), mean 400 µm (20 cells), height 560–10000 µm (25–400 cells), mean 5000 µm (250 cells); homogeneous to heterogeneous type III, multiseriate portion of ray composed of procumbent cells, with 1–3 rows of procumbent to square marginal cells.

Imperforate tracheary elements: fibre-tracheids, distribution random; tangential diameter 154–25 µm (length indeterminate because of poor preservation); approaching thick-walled; distinctly bordered pits on both radial and tangential faces.

Remarks. *Plataninium decipiens* was placed in Platanaceae? by Brett, but Süss and Müller-Stoll (1977) exclude it from their list of fossil woods allied to *Platanus* (as they do for Brett's *Platanus* sp.). The problematic affinities of platanoid woods have also been discussed at length by Greguss 1969; Page 1967–8, 1981; Scott and Wheeler 1982; Wilkinson 1984; Wheeler *et al.* 1977.

The present specimen differs from the holotype mainly in the absence of growth rings and in vessel density and ray width. Brett's description includes variation of this nature between the holotype and paratype. The holotype has obscure growth rings, vessel density of 30/mm² and rays 2–18 cells wide, whilst the paratype has no growth rings, a vessel density of 42/mm² and rays 4–25 cells wide. In comparison V.62922 has no growth rings, vessel density of 12–19 cells/mm² and rays 4–30 cells wide. This can almost certainly be accounted for by known variation within single species of fossil and living woods. A comparable range of variation is shown by *Plataninium haydeni* Felix (1896) emend. Wheeler, Scott and Barghoorn 1977 from the Eocene of Yellowstone and Clarno (Wheeler *et al.* 1977). A study of Recent *Platanus* concluded that vessel size, density, and shape of vessels is extremely variable within single species (Süss and Müller-Stoll 1975).

The specimen described in this paper was found loose, presumably weathered out from the underlying Reading Beds. In comparison with another wood (*Ulmium* sp., BMNH V.24) collected *in situ* from Reading Beds exposed in a railway cutting at Shaw near Newbury, Berkshire (about 26 km from Farnborough), the similar colour and gross preservational features suggest that V.62922 is also from the Reading Beds.

Crane (1978) noted that platanoid leaves occur in clay and silt pockets of the Reading Beds at Cold Ash Quarry near Newbury.

Family EUPTELEACEAE? Wilhelm (1910), FAGACEAE? Dumortier (1829), ICACINACEAE? Miers (1851) or PLATANACEAE? Dumortier (1829)

Plataninium brettii sp. nov.

Plate 71, figs. 1–4

Diagnosis. [Secondary xylem]. Distinct growth rings 2–3 mm wide. Vessel distribution diffuse porous, 50/mm², with tangential alignment; mainly solitary with a few radial groups up to 4 cells, vessel tangential diameter mean 35 μ m, perforation plates scalariform, usually with 15 fine bars, intervacular and vessel to ray pitting opposite to alternate, round, elongate or approaching scalariform. Rays 2–5 per tangential mm, of two distinct sizes, multiseriate (6 or more cells wide) or uniseriate, multiseriate ray mean width 80 μ m (9 cells), mean height 3000 μ m (168 cells), uniseriate mean width 15 μ m, mean height 600 μ m (24 cells), heterogeneous type II–III, uniseriate margins of 4 or more cells, uniseriate rays composed of procumbent and upright cells. Fibre-tracheids with distinctly bordered pits.

Derivation of name. After Dr D. W. Brett who began the description of British Tertiary dicotyledonous wood.

Holotype. BM(NH) V.25264, slides BM(NH) V.25264\$1–3 (Pl. 71, figs. 1–4).

Locality and horizon. Mull, Inner Hebrides; Palaeocene, Interbasaltic Beds, Plateau Volcanics Series.

Description. Single silicified piece measuring 5.7 cm \times 2.5 cm \times 3.5 cm after cutting.

Vessel elements: tangential diameter range 14–56 μ m (many vessels are tangentially compressed and could not be measured; also element length could not be accurately established due to poor preservation), perforation plates with 4–40 bars (Pl. 71, fig. 3; intervacular pitting round to scalariform (near perforation plates), diameter 3–30 μ m, vessel to ray/parenchyma pitting similar to intervacular (Pl. 71, fig. 4); thin-walled tyloses present.

Parenchyma: possibly apotracheal, diffuse-in-aggregate type (very poorly preserved).

Rays: uniseriate rays moderately common, sometimes with biseriate portions (Pl. 71, fig. 2); overall width range 10–150 μ m (1–14 cells); uniseriate ray height range 220–2500 μ m (9–85 cells), multiseriate ray height range 1800–6000 μ m (60–216 cells).

Imperforate tracheary elements: fibre-tracheids (diameter and length not determinable due to poor preservation); distinctly bordered pits on radial walls.

Comparison. This wood is closely comparable to extant *Fagus* (Fagaceae), *Platanus* (Platanaceae), *Ottoschultzia* (Icacinaeae) and *Euptelea* (Eupteleaceae). Although *Euptelea*, *Fagus* and *Ottoschultzia* have common uniseriate rays and rays of two sizes, only *Euptelea* and *Ottoschultzia* have entirely scalariform perforation plates. However they also have rays that are heterogeneous I or II and short, numerous uniseriate rays. *Platanus* has some alternate pitting but has homogeneous multiseriate rays with low margins, rare uniseriate rays and simple as well as scalariform perforation plates. Amongst fossil woods the Mull species show most similarity to *Platanoxylon catenatum* Süss and Müller-Stoll (1977) from the Lower to Middle Eocene of Amethyst Mountain, Yellowstone National Park, Wyoming, USA, and *Icacinoxylon laticiphorum* Greguss, 1969 from the Oligocene of Dorog, Hungary. *P. catenatum* has simple and scalariform perforation plates and fewer, shorter, and more homogeneous uniseriate rays whilst *I. laticiphorum* has radial ducts in the rays.

Remarks. The foregoing comparison indicates that *Plataninium brettii* shows similarities to four extant families, of which Platanaceae and Fagaceae are represented by other fossil remains in the Interbasaltic Ardtun Leaf Beds. Crane *et al.* (1988) in a study of the platanaceous leaf *Platanites hebridicus* Forbes (1851) and its associated reproductive structures from these beds have noticed

important differences between these fossils and Recent *Platanus*. Crane *et al.* cite these fossils as further examples of the much greater morphological diversity found in platanaceous reproductive and vegetative remains reported from Cretaceous and Palaeogene strata (Manchester 1986). *Plataninium brettii* may be the wood of the '*Platanites hebridicus* plant' and also reflect this diversity, differing from Recent Platanaceae by possessing: (a) exclusively scalariform perforation plates, (b) heterogeneous rays, (c) common and high uniseriate rays. These features are noted as occurring in wood assigned to fossil Platanaceae but not any of the Recent species by Manchester (1986), Page (1968), and Süss and Müller-Stoll (1977).

Because of doubts over the affinity of *P. brettii* it is not included in the genus *Platanoxylon* Andreánsky (1952) for fossil wood of *Platanus sensu stricto* (Süss and Müller-Stoll 1977), nor in *Icacinoxylon* Schilkina (1956) for fossil wood of unspecialized Icacinaceae, or *Fagoxylon* Stopes and Fujii (1910 emend. Süss 1986) for fossil wood of *Fagus*, or *Euptelea*. Its inclusion in *Plataninium sensu* Page (1968) connotes woods of problematic affinity having solitary vessels, apotracheal diffuse-in-aggregate parenchyma, wide multiseriate rays and scalariform perforation plates showing probable affinity with Eupteleaceae, Fagaceae, Icacinaceae, or Platanaceae.

Family SAPOTACEAE A. L. Jussieu (1789)

Genus SAPOTOXYLON Felix (1882)

Type species. *Sapotoxylon taeniatum* Felix (1882) from the Tertiary of Bavaria, West Germany.

Sapotoxylon atkinsoniae sp. nov.

Plate 69, figs. 7–9; Plate 70, figs. 1 and 9; Table 4

Derivation of name. After the collector, Mrs P. Atkinson.

Holotype. BM(NH) V.62706, slides V.620706\$1,2 (Pl. 69, figs. 7 and 8).

Paratypes. BM(NH) V.62704, slides V.62704\$1,2 (Pl. 70, figs. 1 and 9); V.62705, slides V.62705\$1,2 (Pl. 69, fig. 9).

Locality and horizon. Collected loose from the beach, Isle of Sheppey, Kent; Lower to Middle Eocene, London Clay.

Diagnosis. [Secondary xylem]. Vessel distribution diffuse porous, 20–25/mm², solitary or commonly in radial multiples of 2–4, tangential diameter means 63–98 μ m, element length means 360–420 μ m, perforation plates simple, intervacular pitting alternate, bordered, diameter 3–5 μ m, vessel to ray/parenchyma pitting similar to intervacular pitting. Parenchyma as apotracheal bands, 1–3 per radial mm, moderately continuous, 1–4 cells wide. Rays are 1–3 cells wide with common uniseriate rays, some rays with two biseriate portions per ray, often the same width as uniseriate portions, width means 22–25 μ m (1–2 cells), uniseriate ray height means 150–200 μ m (4–7 cells), multiseriate ray height means 280–590 μ m (10–23 cells), heterogeneous II, the multiseriate rays with marginal rows of 1–4, square to upright cells, the uniseriate rays consisting of square and upright cells. Fibres libriform and thin-walled.

Description. Three calcified specimens, the largest (V.62704) 25 cm diameter by 12 cm thick. Much of the wood has been destroyed by *Teredo* burrows. No evidence of incremental growth.

Vessel elements (Table 4): solitary (30%) and in radial multiples of 2–4, mostly 2 (50%) (Pl. 69, fig. 7); some vessels filled with a brown substance that was probably gum.

Parenchyma: apotracheal, mainly as moderately continuous bands that can end abruptly; broadly spaced (Pl. 69, figs. 7 and 8); some diffuse cells; chambered cells present, with up to four crystalliferous chambers (Pl. 70, fig. 9).

TABLE 4. Variability in quantitative features of *Sapotoxylon atkinsoniae* sp. nov. TD = tangential diameter; EL = element length; RW = ray width; MH = multiseriate height; UH = uniseriate height.

	V.62704	V.62705	V.62706
Vessels			
TD mean (μm)	98	80	63
TD range	70–140	48–120	42–98
EL mean (μm)	360	420	400
EL range	250–470	310–580	280–560
Rays			
RW mean (μm)	22	23	25
RW range	16–27	15–30	16–30
RW range (cells)	1–2	1–2	1–2
MH mean (μm)	280	580	560
MH range	180–420	200–980	120–440
MH mean (cells)	10	23	12
MH range	7–19	6–35	3–20
UH mean (μm)	150	200	—
UH range	120–210	110–600	66
UH mean (cells)	4	7	—
UH range	3–10	2–14	2

Rays (Table 4): 7–9 per tangential mm; mainly biseriate with fairly common uniseriate rays except V.62706 where uniseriate rays are very rare; biseriate portions composed of procumbent cells (Pl. 69, fig. 9; Pl. 70, fig. 1).

Imperforate tracheary elements: libriform fibres in radial files; diameter 7–21 μm (length not determinable due to poor preservation); pitting not observed.

Comparison. Certain genera within extant Sapotaceae and Rubiaceae show the greatest similarity to this fossil. In Rubiaceae apotracheal parenchyma bands four cells in width are present in species of *Alibertia*, *Craterispermum*, *Fernelia*, *Jackia* and *Stenostomum*. A specimen of *Alibertia edulis* Rich (1830) in the collection at Kew possesses bands 1–3 mm apart but it has a much higher percentage of solitary vessels and longer, heterogeneous I rays. Fibres in Rubiaceae usually also have bordered pits (fibre-tracheids), although these may be small and indistinct. No pitting could be observed on the fibres in the Sheppey fossils (SEM examination of fossil fragments may resolve such detail (Crawley 1988) but is prevented in this case by the nature of the specimens). In Sapotaceae some species in the genera *Argania*, *Manilkara*, *Matichodendron*, *Minusops*, *Neoxythece*, *Pouteria* and *Sandwithiodoxa* have similar apotracheal bands but in all the species examined these were up to 1 mm apart not 1–3 mm apart. However, in vessel distribution, parenchyma type, and ray composition the fossils show the greatest similarity to Sapotaceae, especially *Urbanella excelsa* (Smith) Aubréville (1962) as figured by Kukachka (1982).

Two species of fossil Sapotaceae possess apotracheal banded parenchyma: *Palaeosideroxylon flammula* Grambast-Fessard (1968) from the Upper Miocene of Castellane, south-east France and *Sapotoxylon taeniatum* Felix (1882) from the Tertiary of Bavaria, West Germany. Both are distinct from the Sheppey woods because *P. flammula* has vessels in a tangential 'flame'-like arrangement and *S. taeniatum* has larger vessels (180 μm diameter) and 1–3 seriate rays.

Remarks. Inclusion in the genus *Sapotoxylon* Felix (1882), indicates fossil woods of sapotaceous affinity but not closely comparable to any extant genus. Sapotaceae are also represented in the flora of the London Clay by four species of fruits and seeds belonging to the genera *Sapotocarpum* Reid and Chandler (1933) (three spp.) and *Sapotispermum* Reid and Chandler (1933). As was found for

TABLE 5. Comparison of quantitative features of *Tarrietioxylon hazzeldinewarrenii* sp. nov. and *T. cf. hazzeldinewarrenii*. TD = tangential diameter; EL = element length; MW = multiseriate width; MH = multiseriate height; UH = uniseriate height.

	V.28223	V.27120	V.27511	V.28222
Vessels				
TD mean (μm)	196	160	140	158
TD range	105–245	102–280	84–170	104–196
EL mean (μm)	590	380	—	—
EL range	240–840	170–700	—	—
Rays				
MW mean (μm)	140	245	245	280
MW range	70–210	70–280	75–280	80–315
MW range (cells)	4	6	6	7
MW range	2–6	2–8	2–7	2–10
MH mean (μm)	1520	900	1100	980
MH range	560–3360	400–1600	340–1760	400–1620
MH mean (cells)	34	24	30	28
MH range	13–68	11–36	12–40	11–38
UH mean (μm)	693	220	330	280
UH range	420–980	160–300	220–440	160–550
UH mean (cells)	9	4	6	5
UH range	6–14	3–7	5–9	3–9

the woods only the family affinity of these fruits and seeds seems clear (Reid and Chandler 1933). Today Sapotaceae are mainly tropical and of wide distribution. They form an important part of the ecosystem of the neotropics, constituting up to 25% of timber volume in the Amazon Basin (Kukachka 1982).

Family STERCULIACEAE Bartling (1830)
Genus TARRIETIOXYLON Kräusel (1922)

Type species. *Tarrietioxylon sumatrense* Kräusel (1922) from the Middle Miocene of Muara Bungin am Sungai Pobungo, Indonesia.

Tarrietioxylon hazzeldinewarrenii sp. nov.

Plate 72, figs. 7, 9–11; Table 5

Derivation of name. After the collector, Mr S. Hazzeldine-Warren.

Holotype. BM(NH) V.28223, slides V.28223S1–4 (Pl. 72, figs. 9–11).

Locality and horizon. St Albans Sand Company Pit, Nazeing, near Harlow, Essex; Upper Palaeocene, Reading Beds.

Diagnosis. [Secondary xylem]. Vessels diffuse porous, 3–6/mm², mainly in radial multiples of 2 (70%), mean tangential diameter 196 μm , mean length 590 μm , perforation plates simple; pitting with coalescent apertures, intervascular and vessel to ray/parenchyma pitting alternate, bordered, 5–6 μm diameter. Parenchyma paratracheal and apotracheal; paratracheal as vasicentric sheaths 1–4 cells broad, apotracheal as diffuse and diffuse-in-aggregate uniseriate chains. Rays 4–6 per tangential mm, of two distinct sizes: 4–5 seriate or uniseriate, the uniseriate rays common and approaching a storied condition; overall width range 30–210 μm (1–6 cells), uniseriate width mean 30 μm , multiseriate width mean 140 μm (4–5; cells), uniseriate ray height mean 693 μm (9 cells),

multiseriate ray height mean $1520\ \mu\text{m}$ (34 cells), heterogeneous type II–III, multiseriate rays with 1–2, square to upright, marginal cells, uniseriate rays composed of procumbent, square and upright cells. Sheath cells present. Fibres libriform and thin-walled.

Description. A single silicified piece, $5\text{ cm} \times 4\text{ cm} \times 2\text{ cm}$ before cutting. Growth rings only weakly defined.

Vessel elements (Table 5): solitary and in radial multiples of 2–6 (Pl. 72, fig. 9), some irregular clusters present at growth-ring boundary; vessel to ray/parenchyma pitting similar to intervacular but with a few more elongate apertures occasionally present (Pl. 72, fig. 11); some vessels have dark contents, probably gum (and also the remains of fungal hyphae).

Parenchyma: apotracheal as diffuse and diffuse-in-aggregate uniseriate chains linking rays (Pl. 72, fig. 9); locally approaching a storied condition.

Rays (Table 5): width range of uniseriate rays $21\text{--}35\ \mu\text{m}$; those with multiseriate portions composed of procumbent cells (Pl. 72, fig. 10); some cells with very dark contents that were probably gum cysts (Pl. 72, fig. 7).

Imperforate tracheary elements: libriform fibres; diameter $15\text{--}35\ \mu\text{m}$, length not determinable due to poor preservation; thin-walled; pitting not observed.

Comparison. The most similar genera occur in extant Sterculiaceae, particularly species of *Heritiera* and *Tarrietia*. Both genera are recorded as having entirely storied parenchyma, but this feature can be variable as in some specimens of *H. cochinchinensis* (Pierre) Kostermans (1973), *H. simplicifolia* (Masters) Kostermans (1959) and *T. utilis* (Sprague) Sprague (1916) (illustrations in Miles 1978; Normand and Paquis 1976).

Several species in the fossil sterculiacean genera *Sterculioxylon* Kräusel (1939) and *Tarrietioxylon* Kräusel (1922) are closely comparable to the Nazcing wood: *S. dattai* Prakash and Tripathi (1974) from the Upper Miocene of Hailakandi, Assam, India; *S. deccanensis* Lakhnupal, Prakash and Bande (1976) from the Palaeocene/Eocene Deccan Intertrappean Series of Mohgaon, Madhya Pradesh, India; *S. foetidense* Prakash (1973) from the Tertiary of Burma; *S. shahpurenensis* Bande and Prakash (1980), from the Palaeocene/Eocene Deccan Intertrappean Series of Shahpura, Madhya Pradesh, India, and *T. sumatrense* Kräusel (1922), from the Middle Miocene of Muara Bungin am Sungai Pobungo, Indonesia. *S. dattai* has 6–9 seriate rays up to $1500\ \mu\text{m}$ high, and uniseriate rays composed of procumbent cells; *S. deccanensis* has ten seriate rays up to $4800\ \mu\text{m}$ in height. *S. foetidense* has sparse uniseriate rays and a maximum vessel tangential diameter of $400\ \mu\text{m}$, *S. shahpurenensis* has twenty two seriate rays up to $8000\ \mu\text{m}$ high, and *T. sumatrense* has a higher percentage of solitary vessels and multiseriate rays up to 110 cells high.

Remarks. Studies by Manchester (1979, 1980) on the wood of Eocene and Recent Sterculiaceae show that *Chattawayia paliformis* Manchester (1980) does not have noticeably storied axial elements, whilst in *Pterospermum*, the Recent genus it most closely resembles, markedly storied axial elements are usually found. This difference also exists between the Eocene *Triplochitioxylon oregonensis* Manchester (1979) and the Recent *Triplochiton*. Manchester observed that the few extant species without storied axial parenchyma had longer vessel elements as found in the fossils. Similarly *Tarrietioxylon hazzeldinewarrenii* has a longer mean vessel element length than extant *Heritiera* or *Tarrietia* and possesses unstoried parenchyma.

Tarrietioxylon cf. *hazzeldinewarrenii*

Plate 72, fig. 8; Table 5

Material. BM(NH) V.27511, slides V.27511S1–3; V.27512, slide V.27512S1; V.27120, slides V.27120S1–4; V.28222, slides V.28222S1–3 (Pl. 72, fig. 8).

Locality and horizon. Nazcing, near Harlow, Essex; Upper Palaeocene, Reading Beds.

Collection details. Collected by Mr S. Hazzeldine-Warren.

Description. Three silicified pieces, the largest 16 cm × 12 cm × 5 cm before cutting. Growth-rings indistinct (V.27512 not used due to poor preservation).

Vessel elements (Table 5): diffuse porous, solitary and in radial multiples of 2–4, mostly 2 (60%), occasionally in clusters; 5–8/mm²; perforation plates simple; pitting with coalescent apertures, intervascular pitting alternate, bordered, 4–6 µm diameter, vessel to ray/parenchyma pitting similar to intervascular; dark deposits in some vessels is probably gum (fungal hyphae also present).

Parenchyma: paratracheal, as vasicentric sheaths 1–4 cells thick, apotracheal as diffuse and diffuse-in-aggregate type.

Rays (Table 5): 2–4 per tangential mm; of two distinct sizes: 6–7 seriate and uniseriate; uniseriate rays moderately common (Pl. 72, fig. 8); homogeneous to heterogeneous type III, rays with multiseriate portions composed of procumbent cells, marginal rows of 1–2 cells, upright, square or procumbent, uniseriate rays composed of procumbent, square or upright cells; sheath cells present but uncommon; cells with dark contents common.

Imperforate tracheary elements: libriform fibres; diameter 20–38 µm (length indeterminable due to poor preservation); thin-walled; pitting not observed.

Remarks. *Tarrietioxylon hazzeldinewarrenii* and *T. cf. hazzeldinewarrenii* are anatomically similar but show some differences in the rays and in vessel dimensions. (Pl. 72, figs. 7 and 8, Table 5). *T. cf. hazzeldinewarrenii* has almost homogeneous rays, 1–10 cells broad, with fewer uniseriate rays. Bande and Prakash (1983) describe intraspecific ray width variation in trunkwood of extant *Sterculia* (Sterculiaceae) in relation to *Sterculioxylon shalpurensis* and *S. cf. shalpurensis*. Similar variation also occurs between branch, trunk and root wood within a single tree. Fegel (1941) observed that the largest ray volume is found in the roots of hardwoods. However Barefoot and Hankins (1982) stated that assigning fragmented fossil wood to their relative positions on the plant is often impossible. Certainly a necessarily cautious approach is warranted but a large sample size can justify an intraspecific approach to variation whilst not actually having to assign to a part of the tree. A further alternative is specific variation. Some species of *Heritiera* have homogeneous rays with no sheath cells whilst others have heterogeneous rays with sheath cells. Until a larger sample of material is available the fossils are treated as probably the same species but with some reservations.

A single species of sterculacean fructification is known from the Lower Tertiary of Britain, *Sphinxia ovalis* Reid and Chandler (1933) from the Eocene, London Clay. Present day Sterculiaceae are tropical to sub-tropical in distribution.

CONCLUSIONS

The Palaeocene woods of Eigg and Mull have distinct growth rings; the Palaeocene woods from England, with the exception of *Ulmium elliottii*, do not. This difference suggests different environments for the two groups of woods. Trees of seasonal climates generally produce distinct growth rings. Although some rain forest trees produce distinct growth rings (Alvim 1964), it is suggested that the Mull and Eigg woods grew in a seasonal environment. Seasonality for the Eigg flora is further indicated by the semi ring porous vessel distribution seen in *Eiggoxylon*, as ring porosity is believed to be an adaptation to seasonal variation (Gilbert 1940). A further palaeoecological distinction between these two groups of fossil woods is evident from their vulnerability indices (Table 6). Such indices result from dividing mean vessel diameter by mean vessel density and provide an indication of the potential resistance of the xylem to the formation of intravessel air embolisms or, if these are formed, the potential to restrict the resulting loss of function (Carlquist 1977). These embolisms are produced by freezing or transpiration stress. The Scottish woods have low vulnerability indices, indicating an environment of high water stress, which would be in keeping with the temperate climate suggested for the Mull Flora (Seward and Holttum 1924). However the woods from south-east England have high to very high indices indicating an environment lacking water stress, a situation found today in humid tropical and sub-tropical regions. These findings support the frostless climate proposed by Daley (1972) for the early Tertiary of southern England. The values can be compared to Carlquist's average vulnerability index for

TABLE 6. Vulnerability indices of fossil dicotyledonous woods from Britain.

<i>Cercidiphylloxylon spenceri</i>	0.3
<i>Plataninium brettii</i>	0.7
<i>Eigoxylon reidii</i>	1.9
<i>Edenoxylon? atkinsoniae</i>	3.5
<i>Sapotoxylon atkinsoniae</i>	3.5
<i>Plataninium decipiens</i>	4.6
<i>Ulmium elliotii</i>	15.5
<i>Ulmium? sp.</i>	18.6
<i>Tarrietioxylon cf. hazzeldinewarrenii</i>	25.5
<i>Tarrietioxylon hazzeldinewarrenii</i>	39.2

primitive woods occurring where the water supply is neither scanty nor excessive (mesophytic), calculated as 2.29.

All the woods described here represent mature secondary xylem but in most cases it is not known if they represent branch, trunk or root wood. *Plataninium decipiens* and *Tarrietioxylon hazzeldinewarrenii*/cf. *hazzeldinewarrenii* possibly show variation of this sort. Also the London Clay species *Edenoxylon?* and *Sapotoxylon* are clearly driftwood remains because all specimens are heavily bored by ship-worms (*Teredo* sp.). Therefore it is perhaps more likely that these are the aerial portions of the tree, either large branches or trunks.

This study complements previous knowledge of the Palaeogene vegetation of Britain as known from the fruit, seed and leaf floras from the Ardtun Leaf Beds, London Clay, and Reading Beds. Most of the families represented in this study already had been recorded from these floras. However, purely from the standpoint of fossil wood the families Lauraceae, Sapotaceae and Sterculiaceae are new records from Britain. The occurrence of *Cercidiphylloxylon*, *Ulmium* and *Plataninium* are evidence of the similarity between the Palaeogene woody floras of continental Europe and North America.

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M. CRAWLEY

Department of Palaeontology
British Museum (Natural History)
London SW7 5BD

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